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BY

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(Contribution from Bureau of Plant Industry)

Reprinted from JOURNAL OF AGRICULTURAL RESEARCH

Vol. 34, No. 6 : : : : Washington, D. C., March 15, 1927

PUBLISHED BY AUTHORITY OF THE SECRETARY OF AGRICULTURE, WITH THE COOPERATION OF THE ASSOCIATION OF LAND-GRANT COLLEGES

U. S. GOVERNMENT PRINTING OFFICE : 1927

All correspondence regarding articles from State experiment stations should be addressed to R. W. Thatcher, Agricultural Experiment Station, Geneva, N. Y.

Published on the first and fifteenth of each month. This volume will consist of twelve numbers and the Contents and Index.

Subscription price: Domestic, $4.00 a year (two volumes)
Single numbers, 20 cents
Foreign, $5.25 a year (two volumes)
Single numbers, 25 cents

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A MORPHOLOGIC AND BIOMETRIC COMPARISON OF CRONARTIUM RIBICOLA AND CRONARTIUM OCCIDENTALE IN THE AECIAL STAGE [1]

By REGINALD H. COLLEY and CARL HARTLEY, *Pathologists*, and MINNIE W. TAYLOR, *formerly Junior Pathologist, Office of Forest Pathology, Bureau of Plant Industry, United States Department of Agriculture* [2]

INTRODUCTION

Ever since the piñon blister rust, *Cronartium occidentale* Hedgcock, Bethel, and Hunt (*5*),[3] was discovered to be widespread in certain sections of the Western States, the question has been raised as to whether it was really distinct from the white pine blister rust, *Cronartium ribicola* Fischer. The former is relatively innocuous, attacking—so far as is known—only the nut pines; but the latter is a particularly destructive parasite infecting the valuable 5-needled pines. The uredinial and telial stages of both forms occur on members of the genus Ribes. A recent study (*3*) has shown that the urediniospores of the two species are very close together biometrically but fairly consistently different, and that the size and shape of the spores are reasonably reliable criteria for diagnosis. The purpose of the present paper is to submit the evidence of morphologic and biometric differences in the aecial stages. These differences appear to be both significant and easily recognized.

MATERIAL

The chief source of material was the office collection. In addition, specimens which had been specially preserved in formalin-alcohol (6 c. c. full strength [37 per cent] commercial formaldehyde to 94 c. c. of 70 per cent alcohol) and specimens fresh from the field were used. Slides were made from these preserved and fresh specimens; and slides which had been prepared in previous work on the morphology and cytology of *Cronartium ribicola* (*1*) were carefully restudied.

Herbarium material only was selected for the biometric study of the aeciospores and peridia. For each species apparently representative specimens, with as wide a locality and time of collection range as possible, were chosen. Most of the *Cronartium ribicola* material was on the one host *Pinus strobus* L., although there were three specimens on *P. monticola*, but the *C. occidentale* selections were about equally divided between *P. edulis* Engelm. and *P. monophylla* Torr. and Frem. The collection data are given in full in Table 1.

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[1] Received for publication Nov. 17, 1926; issued May, 1927.
[2] The writers wish to acknowledge the help rendered by their colleagues, without which it would have been very difficult indeed to carry on the study reported herein. They are also deeply indebted to the members of the Offices of Forest Pathology and Blister Rust Control for specimens, for assistance in the tabulation and analyses of the measurement data, and for much helpful criticism.
[3] Reference is made by number (italic) to "Literature cited," p. 531.

TABLE 1.—*Biometric data on aeciospores of Cronartium ribicola and C. occidentale, based on 100 spores from each specimen*

Host	Locality	Date collected	Length		Width		Mean wall thickness	Ratio: Mean length, mean width
			Mean	Standard deviation	Mean	Standard deviation		
			μ		μ		μ	
Cronartium ribicola:								
Pinus strobus	Dunraven, N. Y	May 20, 1915	24.4	2.3	17.9	1.5	3.36	1.36
Do	East Randolph, Vt	May 18, 1916	25.1	2.0	18.1	1.5	3.04	1.38
Do	Woodstock, Vt	do	24.0	2.0	17.7	1.4	2.98	1.35
Do	Kittery Point, Me	May —, 1917	24.8	2.0	17.9	1.5	2.82	1.38
Do	do	1917	25.2	2.2	19.1	1.4	3.69	1.31
Do	do	May 18, 1917	24.8	2.9	18.5	1.9		1.34
Do	Exeter, N. H	May 24, 1917	25.6	1.8	19.7	1.3	3.69	1.29
Do	Stratham, N. H	May —, 1917	25.9	1.9	19.4	1.4	3.34	1.33
Do	Marlow, N. H	June 14, 1917	24.3	2.9	19.1	1.8	4.18	1.27
Do	Gloversville, N. Y	Sept. —, 1917	23.9	2.4	14.9	1.9		1.60
Do	Kingston, Mass	Mar. 22, 1918	23.3	2.4	17.7	1.5	3.10	1.32
Do	Brunswick, Me	Apr. 30, 1918	24.0	2.0	18.7	1.4	3.20	1.28
Do	Halifax, Mass	May 13, 1918	22.6	1.8	18.2	1.4	3.00	1.24
Do	Maine	May —, 1919	24.1	1.9	19.0	1.5	3.24	1.27
Do	Block Island, R. I	May —, 1920	24.0	2.6	17.7	1.8		1.35
Do	Portland, Me	June —, 1920	24.0	2.0	18.0	2.9		1.33
Do	North Conway, N. H	do	24.9	4.1	16.7	2.1		1.49
Do	Topsfield, Mass	Mar. —, 1921	22.3	2.1	18.1	2.0		1.23
Do	do	Mar. 27, 1921	24.0	2.2	18.7	1.5	3.17	1.28
Do	Block Island, R. I	Apr. 6, 1921	22.0	1.9	17.2	1.5	2.81	1.27
Do	South Deerfield, N. H	May —, 1922	23.7	2.2	18.3	1.8	3.23	1.29
Do	Vancouver, B. C	Mar. —, 1922	22.4	2.8	16.8	1.6	2.97	1.33
Pinus monticola.	North Vancouver, B. C.	June —, 1922	25.9	2.2	19.6	1.6	4.29	1.32
Do	do	June 7, 1922	26.3	2.0	20.6	1.6	[1] 4.50	1.27
Do	Vancouver, B. C	June 9, 1922	24.3	2.0	19.2	1.6	[1] 4.17	1.26
Constants computed from specimen means.			24.2	1.11	18.3	1.14	3.41	[2] 1.32
Cronartium occidentale:								
Pinus edulis	Bayfield, Colo	May 19, 1918	27.2	2.6	18.9	1.8	4.01	1.43
Do	Trimble Hot Springs, Colo.	June 23, 1918	25.7	2.1	18.6	2.2	3.48	1.36
Do	Mancos, Colo	June 28, 1918	26.5	2.3	19.3	2.0	3.51	1.37
Do	do	June 29, 1918	27.4	3.0	20.0	2.1	3.71	1.37
Do	Mesa Verde National Park, Colo.	July —, 1918	25.8	2.6	19.0	2.4		1.35
Do	Glenwood Springs, Colo.	May 28, 1919	25.7	2.4	18.8	1.4	3.62	1.36
Do	Bayfield, Colo	Oct. 15, 1920	28.8	3.3	19.4	2.4	4.29	1.48
Do	Mancos, Colo	Oct. 16, 1920	23.6	2.3	18.5	1.8	3.64	1.27
Pinus monophylla.	Minden, Nev	May —, 1920	26.7	2.7	16.8	2.7		1.59
Do	do	May 20, 1920	28.1	3.3	20.9	2.4	4.39	1.34
Do	do	May 22, 1920	28.5	2.7	20.6	1.6	4.75	1.38
Do	do	May 30, 1920	27.1	2.9	18.9	1.6	3.97	1.43
Do	Bridgeport, Calif	May 31, 1920	27.8	3.0	18.3	2.0	3.31	1.51
Do	Walker Canyon, Calif	do	27.1	2.5	18.0	1.8	3.78	1.50
Do	Minden, Nev	June —, 1920	27.1	2.9	18.2	2.2		1.49
Do	do	Aug. —, 1920	26.3	2.6	18.9	2.6		1.39
Do	Bethel Collection	Sept. —, 1920	26.4	2.8	19.0	2.2		1.39
Do	Bridgeport, Calif	Sept. 12, 1920	28.1	2.5	20.5	2.5	4.03	1.37
Do	Sweetwater, Nev	Sept. 14, 1920	27.0	2.9	19.6	2.2	3.40	1.37
Do	Carter's Station, Nev	June —, 1921	25.3	3.4	18.1	2.3		1.39
Do	Bridgeport, Calif	May 31, 1920	27.5	3.7				
Constants computed from specimen means.			26.8	1.18	19.0	.95	3.85	[2] 1.41

[1] Based on 200 spores.

[2] Geometric means of the above ratios.

METHODS

SECTIONING, STAINING, AND MOUNTING

The killing, sectioning, staining, and mounting methods described in the earlier paper on *Cronartium ribicola* (*1*) were followed in preparing slides for the study of the mycelium in the bark and wood, and the young aecia. The mature peridia were sectioned for the measurement study and for observations on comparative morphology either with hand razors or on an ether freezing microtome. The use of two sections of a Lima bean for holding the peridia, suggested by N. A. Cobb, made the sectioning process comparatively easy in spite of the brittle character of the objects. The hardness of the Lima bean was adjusted by soaking and redrying until it was just right for the job.

Aeciospores were shaken out of the aecia (not scraped out) or picked up on a knife blade from the bottom of the packet containing the specimen, and mounted in the same glycerin and glycerin-jelly media that were used in the study of the urediniospores (*3*).

Fragments and sections of the peridia were mounted in the same way.

It will be noted that the method of getting the aeciospores into the mounts assured both mature spores and a fairly good sampling of the spores from any particular specimen. Each mount made by shaking the spores out of the aecia into the mounting media presumably contained spores from several aecia; and each mount made from the mass of spores which were lying loose in the herbarium packet presumably contained a mixture of spores from all the opened aecia on the specimen.

MEASURING

The great majority of the spores were measured by means of a projection apparatus (*2*). The images of the spores, at a magnification of 1,000 diameters, were thrown on a white field; and those images which fell within a 4-inch circle in the center of this field were measured to the nearest millimeter with a white-face millimeter scale.

In all of the measurement work the mount was moved across the field of vision systematically by means of a mechanical stage. One hundred spores were measured from each of the specimens of each species. The thickness of the thickest visible part of the side spore wall was measured on 100 spores of each of 19 specimens of *Cronartium ribicola* and 14 specimens of *C. occidentale*.

The tubercles on the aeciospores were measured with a filar micrometer.

Measurements of the peridial cells, also made with a filar micrometer, were limited to the cells of the outer layer of the peridium. The walls measured were the outer walls of these same cells. The measurement results are presented in Tables 1 to 6.

TABLE 2.—*Biometric data on the tubercles on the aeciospores of Cronartium ribicola and C. occidentale, based on 100 tubercles from each specimen*

Host	Locality	Date collected	Length		Width		Ratio: Mean length, mean width
			Mean	Standard deviation	Mean	Standard deviation	
Cronartium ribicola:			μ		μ		
Pinus strobus	Dunraven, N. Y.	May 20, 1915	1.64	0.35	1.16	0.24	1.41
Do	Exeter, N. H.	May 24, 1917	1.56	.25	1.15	.22	1.35
Do	Kingston, Mass.	Mar. 22, 1918	1.52	.28	1.10	.22	1.38
Do	Block Island, R. I.	May —, 1920	1.47	.28	1.06	.18	1.38
Do	Topsfield, Mass.	Mar. —, 1921	1.39	.26	1.04	.17	1.33
Pinus monticola	North Vancouver, B. C.	June —, 1922	1.51	.32	1.08	.21	1.39
Do	do	June 7, 1922	1.53	.45	1.11	.21	1.37
Constants computed from specimen means.			1.52	.071	1.10	.041	[1] 1.37
Cronartium occidentale:							
Pinus edulis	Bayfield, Colo.	May 19, 1918	2.26	.53	1.31	.24	1.72
Do	Mancos, Colo.	June 29, 1918	2.30	.69	1.36	.29	1.69
Pinus monophylla	Minden, Nev.	May 22, 1920	2.21	.54	1.33	.26	1.66
Do	do	May —, 1920	2.26	.83	1.34	.29	1.68
Do	Carters Station, Nev.	June —, 1921	2.40	.62	1.32	.27	1.81
Constants computed from specimen means.			2.29	.063	1.33	.017	[1] 1.71

[1] Geometric means of the above ratios.

TABLE 3.—*Biometric data on the outer layer of peridial cells in the aecia of Cronartium ribicola and C. occidentale, based on 100 cells from each specimen*

Host	Locality	Date collected	Length		Width		Wall		Ratio: Mean length, mean width
			Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	
Cronartium ribicola:									
Pinus strobus			μ 42.7	6.0	μ 31.5	7.3	μ 6.16	1.24	1.35
Do	Kittery Point, Me.	May —, 1917	42.8	6.6	29.8	5.1	7.25	1.64	1.43
Do			44.1	7.2	29.4	4.5	7.45	1.64	1.50
Do	Kittery Point, Me.	May —, 1917	38.8	8.4	26.5	4.5	6.19	1.17	1.46
Do	do	do	42.8	6.4	28.7	4.5	6.82	1.10	1.49
Pinus monticola.	North Vancouver, B. C.	June 7, 1922	38.4	6.6	27.2	5.9	6.52	-------	1.41
Do	Vancouver, B. C.	June 9, 1922	43.7	6.7	30.4	5.7	7.74	-------	1.43
Do	North Vancouver, B. C.	June, —, 1922	38.2	6.9	24.3	5.1	9.12	-------	1.57
Constants computed from specimen means.			41.4	2.35	28.5	2.19	7.16	.919	[1] 1.45
Cronartium occidentale:									
Pinus edulis	Bayfield, Colo.	May 19, 1918	27.0	3.4	20.6	3.6	4.48	.81	1.31
Do	do	do	25.5	3.5	18.0	3.7	4.14	.90	1.41
Pinus monophylla.	Bridgeport, Calif.	May 31, 1920	28.7	4.9	18.7	2.9	5.00	.88	1.53
Do	do	do	27.8	3.7	18.6	3.5	4.95	1.02	1.49
Do	do	do	28.1	4.8	19.6	2.8	4.84	.82	1.43
Constants computed from specimen means.			27.4	1.10	19.1	.91	4.68	.326	[1] 1.43

[1] Geometric means of the above ratios.

TABLE 4.—*Biometric data on the "concomitant" cells in the aecia of Cronartium occidentale, based on 100 cells from each specimen*

Host	Locality	Date collected	Length		Width		Mean wall thickness	Ratio: Mean length mean width
			Mean	Standard deviation	Mean	Standard deviation		
			μ		μ		μ	
Pinus edulis	Bayfield, Colo.	June 19, 1918	21.8	3.0	17.2	2.5	4.64	1.26
Pinus monophylla	Bridgeport, Calif.	May 31, 1920	21.9	2.3	18.5	2.1	4.92	1.18
Do	do	do	21.5	2.4	18.0	2.4	4.35	1.19
Do	do	do	22.4	2.5	17.8	2.0	4.56	1.25
Do	Minden, Nev.	June —, 1920	22.0	2.5	18.0	2.4	4.54	1.22
Constants computed from specimen means.			21.9	.29	17.9	.42	4.60	[1] 1.22

[1] Geometric mean of above ratios.

TABLE 5.—*Biometric constants for Cronartium ribicola and C. occidentale, computed from the populations of specimen means*

Dimensions measured	Cronartium ribicola					Cronartium occidentale					Difference between the two fungi			
	Number of specimens	Mean	Probable error of the mean	Probable deviation of a single specimen	Coefficient of variability	Number of specimens	Mean	Probable error of the mean	Probable deviation of a single specimen	Coefficient of variability	Difference between means	Probable error of the difference	Ratio: Difference, error	Diagnostic division point
Aeciospores:														
Length	25	24.2	0.15	0.76	4.6	21	26.8	0.18	0.81	4.4	2.6	0.23	11.3	25.5
Width	25	18.3	.16	.79	6.2	20	19.0	.15	.65	5.0	.7	.21	3.8	18.7
Wall	19	3.41	.081	.353	14.9	14	3.85	.074	.279	10.4	.440	.109	4.0	3.66
Length / Width	25	[1] 1.32	.010	.053	5.8	20	[1] 1.41	.011	.050	5.1	.09	.015	5.3	1.365
Aeciospore tubercles:														
Length	7	1.52	.019	.051	4.7	5	2.29	.022	.048	2.8	.77	.029	26.6	1.92
Width	7	1.10	.011	.029	3.7	5	1.33	.006	.013	1.3	.23	.012	19.3	1.26
Peridial cells:														
Length	8	41.4	60	1.70	5.7	5	27.4	.37	.83	4.0	14.0	.70	20.0	31.9
Width	8	28.5	.56	1.58	7.7	5	19.1	.31	.68	4.8	9.4	.64	14.7	21.9
Wall	8	7.16	.233	.661	12.8	5	4.68	.110	.246	7.0	2.48	.257	9.6	5.33

[1] Geometric means.

TABLE 6.—*Summary of measurements of aeciospores of Cronartium ribicola and C. occidentale from different hosts*

Host	Number of specimens	Length	Width	Wall thickness
		μ	μ	μ
Cronartium ribicola:				
On Pinus strobus	22	24.0±0.15	[1] 18.1±0.15	[1] 3.24±0.06
On Pinus monticola	3	[2] 25.5± .41	[2] 19.8± .41	[2] 4.32± .14
Differences		1.5± .44	1.7± .44	1.08± .15
Cronartium occidentale:				
On Pinus monophylla	12	27.2± .16	19.0	3.95
On Pinus edulis	8	26.3± .37	19.1	3.61
Differences		.9± .40	.1	.34

[1] Based on 16 specimens only.
[2] Probable errors for these 3-specimen means are not computed from the population of 3 specimens. They are assumed to be the same percentage of the means as would be expected for 3-specimen means from *P. strobus*.

GENERAL OBSERVATIONS

There are certain differences in the habit of *Cronartium ribicola* and *C. occidentale* which are clearly evident to anyone who has had the opportunity to examine representative specimens or to observe the fungi in the field. For example, the pycnia of *C. ribicola* on *Pinus strobus* (*1, pl. 48, fig. B; 7, pl. II, fig. 2*), though occasionally confluent, are usually discrete and conspicuous; whereas the pycnia of *C. occidentale* on *P. monophylla* are made up of broad confluent groups of spore-bearing cells hidden beneath the overlying grayish outer bark.

The typical aecia of *Cronartium ribicola*, as they appear in the smooth soft bark of *Pinus strobus* (*1, pl. 48, fig. B; 5, pl. 55*), are usually separate sori, although occasionally they run together. The peridia, puffed out by the growing aeciospore chains, protrude through the bark—conspicuous bits of evidence that the host is infected. The aecia of *C. occidentale*, particularly on *P. edulis*, are broad confluent spore-producing layers which are more or less completely hidden under the hard bark—the spores massed at a crack in the bark being the only indication of infection. The area of the spore-bearing surface can not be determined until the overlying bark is removed. On young twigs of *P. monophylla*, however, the aecia are small, the peridia protrude, and the general appearance of the infected branch reminds one very strongly of branches of *P. strobus* infected with *C. ribicola*.

Hedgcock, Bethel, and Hunt (*5, p. 414*) are of the opinion that the difference in morphology is not due to the physical difference in the bark of the hosts. In the case of *Cronartium ribicola*, at least, the aecium which develops under the horny, resin-infiltrated bark of the canker area does not expand radially or in any way take on the character of the aecium of *C. occidentale* as it is commonly found under the hard bark of *Pinus edulis*. Aecia on the roots of *P. strobus* appear to be normal in size, shape, and structure (*1, p. 648*). There seems to be no way of ascertaining what form *C. ribicola* would take in the bark of *P. edulis*, or what form *C. occidentale* would take in the bark of *P. strobus*, unless it proves possible to grow the fungi on the hosts indicated. In the face of lack of evidence to the contrary, one is forced to conclude that the difference in habit of the aecia is real and specific. One must also conclude, however, that the type of aecium on the young branches of *P. monophylla* is totally unlike the confluent type on *P. edulis*. The former might be taken for *C. ribicola*, but the latter never. This fact and the data in Table 6 suggest that there may be a varietal difference between *C. occidentale* on *P. edulis* and *C. occidentale* on *P. monophylla*. The question of gradations between the type on the young branches of *P. monophylla* and the type on *P. edulis* must be passed over for the present.

MORPHOLOGIC AND BIOMETRIC COMPARISON

MYCELIAL CHARACTERS

The difference in the character of the bark of *Pinus strobus* and *P. edulis* naturally produces a difference in the appearance of sections of infected tissue. The hyphae and haustoria of the two rusts vary little in habit. The mean diameter of the hyphae in the wood for

both rust species, based on a total of 100 measurements made on six different specimens of each, is 4.9 μ. The walls of the same set of hyphae have a mean thickness of approximately 1 micron. Comparative measurements on the haustoria of the two forms—made on the largest haustoria, and therefore definitely selective—confirmed an impression gained from examination of hundreds of slides that the haustoria of *Cronartium ribicola* are longer than those of *C. occidentale*. The means of 100 measurements (*C. ribicola*, five specimens on *P. strobus; C. occidentale*, four specimens on *P. monophylla*) are as follows:

Haustoria of *C. ribicola*---------- 29.2μ long by 5.4μ in diameter, with a wall 1.1μ thick.
Haustoria of *C. occidentale*------- 25.8μ long by 5.4μ in diameter, with a wall 1.1μ thick.

It is evident that difference in size, as far as these few specimens are concerned, exists only in the length of the haustoria. The difference is six and five-tenths times its probable error. The number of specimens sampled was so small, however, that positive conclusions are not justified. The character of the haustoria may be influenced by the difference in host.

COMPARATIVE MORPHOLOGY OF THE AECIOSPORES OF THE TWO SPECIES

The aeciospores of the two species appear to be very similar under medium power lenses. Under higher powers they are distinctly different. Both species produce characteristic Peridermium spores—obovoid to ellipsoid in shape, with a wall partly smooth and partly coarsely verrucose, as illustrated in Figure 1. Three points of difference in morphology stand out fairly clearly when the spores are compared, namely: The aeciospores of *C. ribicola* (fig. 1, A to G) are slightly smaller than those of *C. occidentale* (fig. 1, H to N); their outline is somewhat more regular; and their tubercles are more regular in shape and more evenly distributed. These differences have been taken into consideration in drawing the figures lettered O and P in Figure 1, which represent mean aeciospores of *C. ribicola* and *C. occidentale*, respectively, constructed on the basis of the mean size figures given in Tables 1 and 2.

One other difference which can not be illustrated in a drawing is a difference in light refraction at the edge of the spore. The wall and tubercles of *Cronartium occidentale* are more refractive than those of *C. ribicola*; and the difference is great enough to enable one familiar with the spores to pick out those of one species from those of the other when both forms are mounted under one cover. The greater refraction in *C. occidentale* appears to be due to the more irregular shape and distribution of the tubercles.

BIOMETRIC COMPARISON OF THE AECIOSPORES

The values given in this and the following sections will be found to differ only slightly from those published in the preliminary report (*4*) on part of the biometric study. The data are summarized in Table 1 and represented graphically in Figure 2. The mean wall thickness refers to the mean of measurements made for each spore at the thickest visible part of the side wall.

The aeciospores reach almost mature size soon after the division of the aeciospore initial into the aeciospore and intercalary cell. For instance, if the spores be numbered from the base of the aecio-

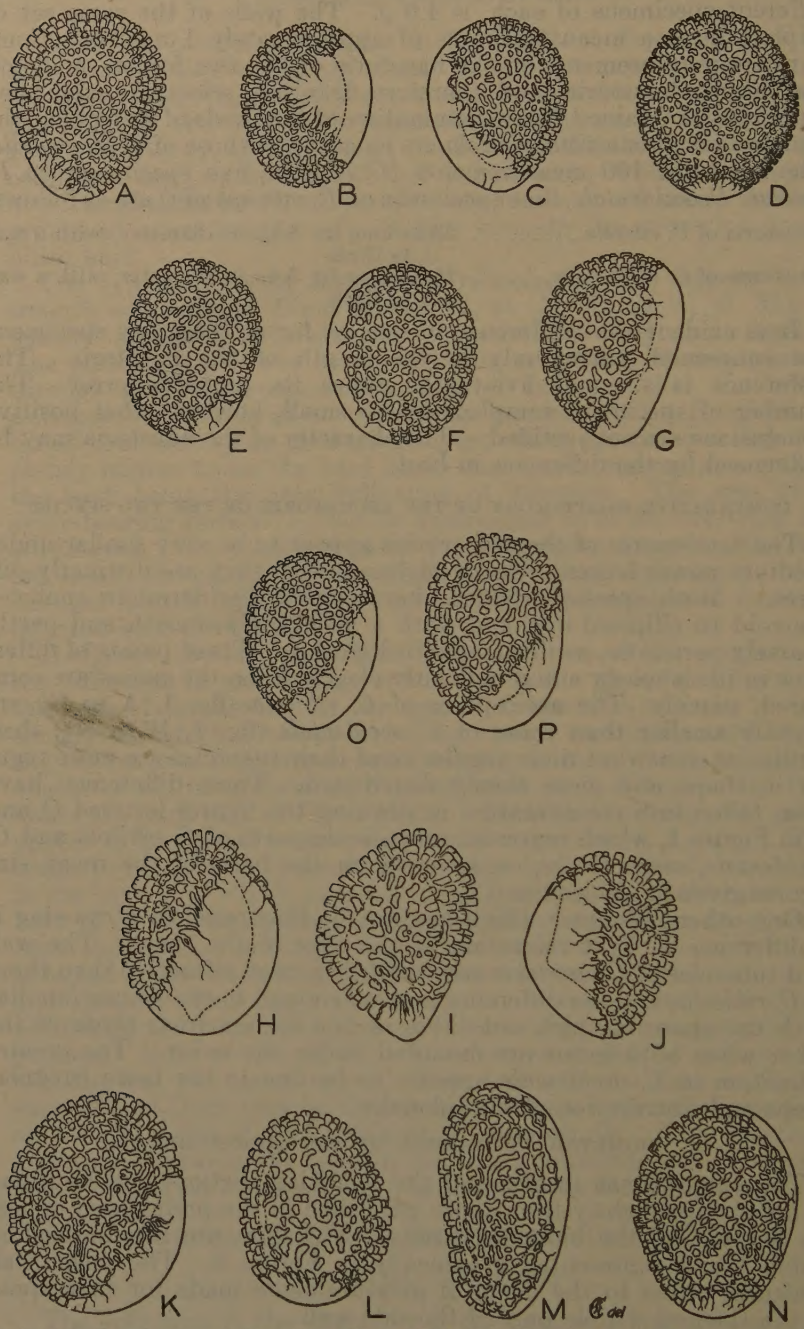

FIG. 1.—A to G, aeciospores of *Cronartium ribicola*, × 900; H to N, aeciospores of *C. occidentale*, × 960; O and P, mean aeciospores of *C. ribicola* and *C. occidentale*, respectively, based on the mean size and shape data given in Tables 1 and 2

spore chain, No. 1 being the youngest, it will be found that the spores in No. 2 position are nearly full size in length, and that those in No. 3 and No. 4 positions are very close to the mean size figures of Table 1, though the walls are still decidedly thinner than in fully matured spores. The following data, from measurements made with a filar

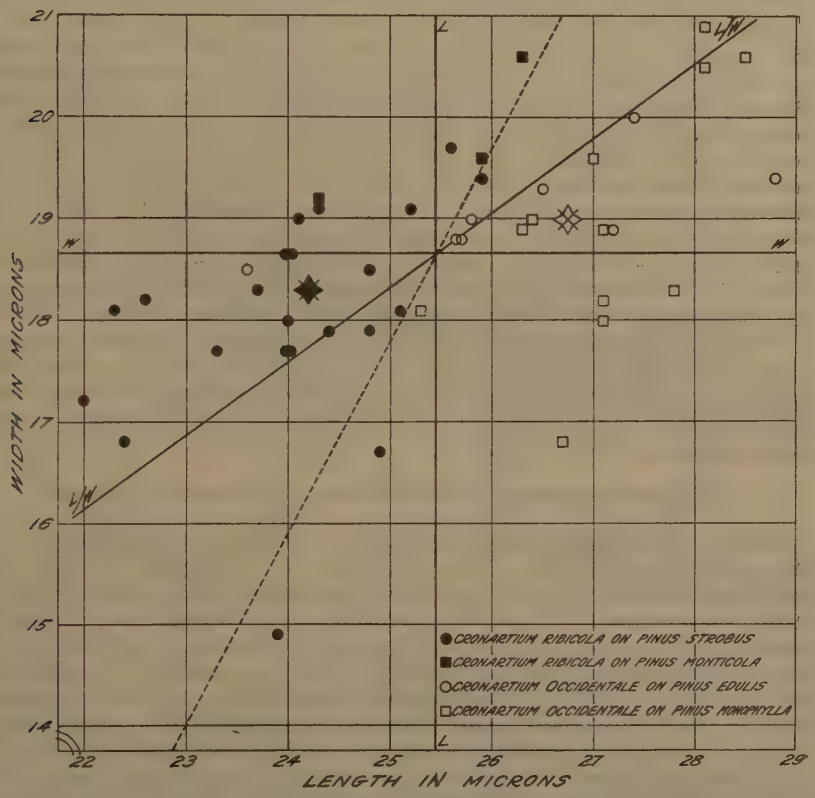

FIG. 2.—*Cronartium ribicola* and *C. occidentale*. Graphic methods for separating two species according to length and width of spores. The points are based on 100-spore means, and each represents a different specimen. The stars indicate the means for the two species. The solid lines are the most probable diagnostic separation lines determined by computation; the line marked W is for width, the line L is for length, and the line marked L/W is for the ratio of length to width. The broken line is located empirically as being apparently the best straight line for separating the two species

micrometer on stained sections mounted in balsam, support the conclusion:

Cronartium ribicola (two specimens, three slides from each):
Second spore in chain.
Means from 26 spores, 23.5×11.7μ, wall 1.9μ.
Third spore in chain.
Means from 20 spores, 24.1×15.0μ, wall 1.9μ.
Fourth spore in chain.
Means from 4 spores, 23.6×13.4μ, wall 1.9μ.
Cronartium occidentale (three specimens, one slide from each):
Second spore in chain.
Means from 26 spores, 26.7×16.6μ, wall 2.7μ.
Third spore in chain.
Means from 20 spores, 28.3×17.3μ, wall 2.8μ.
Fourth spore in chain.
Means from 4 spores, 27.3×17.1μ, wall 2.7μ.

Measurements made on stained spores mounted in balsam are, of course, not directly comparable with the measurement figures in Table 1; and the number of measurements reported is small; but the means are at least indicative. The relatively larger size and thicker wall of the aeciospores of *Cronartium occidentale* are apparently characteristic even before the spores are mature.

Hedgcock, Bethel, and Hunt (*5*) have already called attention to the size of the tubercles on the aeciospores of *Cronartium occidentale* in their description of the species. Morphologic differences in such minute things as tubercles are easily overlooked when one is studying rust spores in a routine way under the medium power of the microscope; yet the recognition of these differences is essential to any true diagnostic description. Data on the size and shape of the aeciospore tubercles are given in Table 2. Length and width in the case of the tubercles mean the long and short dimension, as nearly as they can be measured, of the end views of the tubercles as they appear in Figure 1. The means in the summaries of Table 2 were obtained from measurements of 500 tubercles for *C. occidentale* and 700 for *C. ribicola*, approximately 5 of the most clearly visible tubercles having been measured on each of 20 spores in the case of each of the specimens. The greater length and greater irregularity in shape and distribution of the tubercles in *C. occidentale* is clearly evident in the spores shown in Figure 1.

COMPARATIVE MORPHOLOGY OF THE PERIDA OF THE TWO SPECIES

General observations have indicated a decided difference in the peridia of the two forms. The peridium of *Cronartium ribicola* has been described as thick and persistent in contrast to the inconspicuous, "thin, evanescent" (*5, p. 414*) peridium of *C. occidentale*. Colley's drawings of a section of the peridium of *C. ribicola* (*1, pl. 56, fig. B*) show it as three to four cells thick. Vertical sections through the aecium (*1, pl. 50, fig. B*) show that this multilayered cover extends all over the aecium, and that before the rupture of the bark by the force of the growth of the aeciospore chains the peridium forms a very definite layer between the tips of the young spore chains and the overlying bark and "buffer" tissue. The peridium of *C. occidentale*, whether it remains closely pressed against the overlying bark tissue of *Pinus edulis*, or whether it protrudes through the bark as in the case of infections on young branches of *P. monophylla*, generally appears to be but one cell in thickness. Occasionally a few cells are found in the position of a second, or inner, layer.

The thickness of the cell wall decreases in each layer of cells in the peridium of *Cronartium ribicola* (fig. 3, A); and as a rule the outer wall is thicker than the inner wall of any given cell. The wall thickness remains practically constant for any given cell in *C. occidentale*. Under proper illumination the thick walls are beautifully striated (fig. 3, A and B). The cells retain some of their contents even after the peridia become quite dry. Only rarely are the inner walls of the outer layer of cells marked with tubercles in *C. occidentale;* whereas all the cells are sculptured in the case of *C. ribicola*. The sections shown in the drawings are typical of a large number examined, taken from numerous specimens and localities.

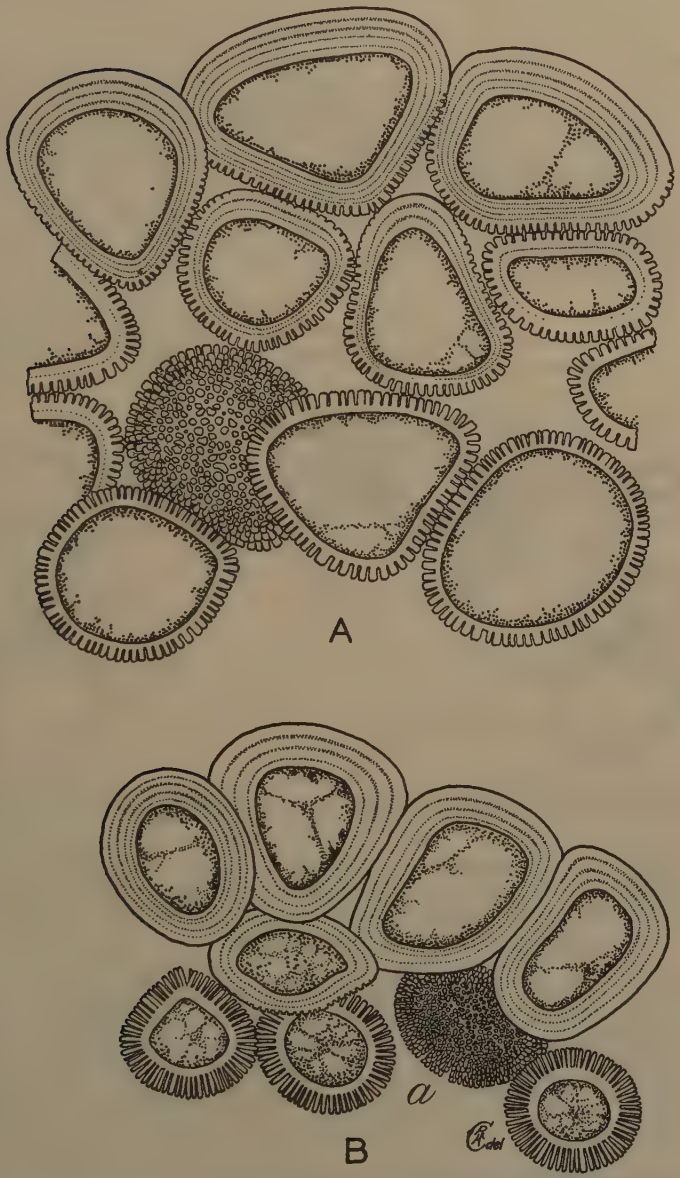

FIG. 3.—A detailed sectional view of small segment of roof of peridium: A, *Cronartium ribicola* on *Pinus strobus;* B, *C. occidentale;* a, "concomitant" cells. × 1,000

A comparison of the illustrations in Figures 4 and 5—sections of the peridia of *Cronartium ribicola* and *C. occidentale*, respectively—brings out the major differences between the two much more clearly than could any description. Particular attention is directed to the cells shown in Figure 3, B, *a*. These "concomitant" cells form a layer in connection with the peridium of *C. occidentale* which may correspond to one of the inner layers of the peridium in *C. ribicola;* but they resemble neither the peridial cells above them nor the spores below. The concomitant cells of *C. occidentale* are so highly refractive that they stand out very clearly when a fragment of the peridium is mounted with the under side toward the objective; and, as a matter of fact, they alone would probably serve to identify the species. If fragments of peridia of *C. ribicola* and *C. occidentale* are mounted side by side under the same cover the two appear to be absolutely distinct. Further work

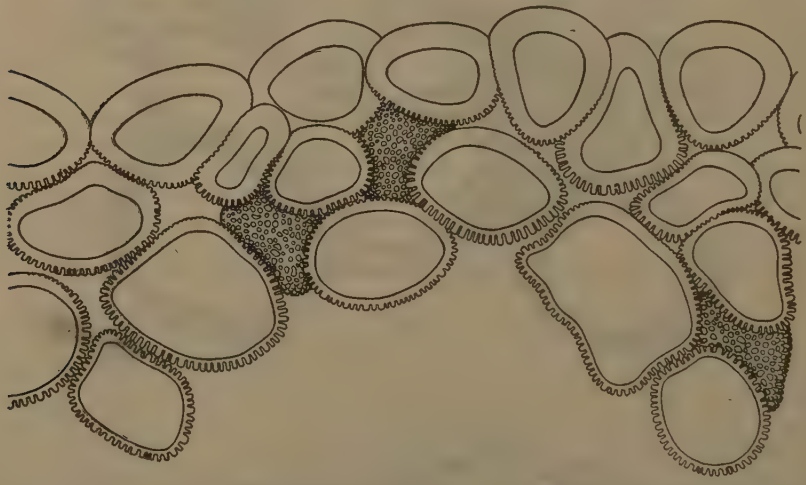

FIG. 4.—Outline drawing of a section of the peridium of *Cronartium ribicola* on *Pinus strobus*, cut near the central or dome region. × 585

will probably show peridial characters to be as important for the Peridermium group as Kern (*6*) has found them to be for Gymnosporangium.

BIOMETRIC COMPARISON OF THE PERIDIAL CELLS

Measuring the size of the peridial cells in surface view was found to be so difficult and the results so generally unsatisfactory that it was decided to use sections of the peridia for the biometric study, and to measure only the long and short dimensions of the outer layer of cells of the peridium, and the thickness of the outer wall of these same cells. In general the cells measured were in the roof rather than in the side walls of the peridia. The results are given in Table 3.

Biometric data on the size of the concomitant cells are given in Table 4. If these figures be compared with the figures for the size of the peridial cells and with the figures for the size of the aeciospores, it becomes evident that the concomitant cells are smaller than either. It is difficult to determine the size of the tubercles on the concomitant cells on account of their small size in end view, and because they are frequently compacted into irregular groups. They average something

less than 1μ in diameter in surface view. The obvious differences between these tubercles and the aeciospore tubercles are illustrated in Figures 1 and 3.

SIGNIFICANCE OF BIOMETRIC DIFFERENCES

The qualitative differences already described show rather clearly that the two rusts are different. To determine whether their morphologic differences are sufficient to warrant giving both of them specific rank, it is necessary to examine the significance of the differences which they exhibit in as many characters as possible.

The differences between the two rusts in the size of the outer layer of peridial cells are so large and consistent as to leave no doubt as to their reality. While the measurement data were obtained only from eight specimens for one species and five specimens for the other, two host species and at least two widely separated localities were represented for each fungus. The 100-cell length means from the different specimens all lie between 25 and 29μ for *Cronartium occidentale*

FIG. 5.—Outline drawing of a section of the peridium of *Cronartium occidentale*, cut near the central or dome region. × 585

and between 38 and 45μ for *C. ribicola*. The differences between the two species in the width and wall thickness of the peridial cells are of nearly the same order of decisiveness.

A glance at Table 2 shows decided differences in the dimensions of the surface view of the tubercles. For the seven specimens of *Cronartium ribicola*, from two hosts and two entirely different regions, the 100-measurement length means are all below 1.65μ; while for the five specimens of the other species, from two hosts and four localities, the length means are all above 2.2μ. The difference in tubercle width is less striking but apparently significant. It is evident that the populations which furnished these measurements of tubercles and peridial cells are quite distinct. Emphatic confirmation of the conclusion reached by inspection is furnished by the probability computations based on the measurements of these units. (See Table 5.)

In the case of the aeciospores themselves, the difference between the species is less obvious. The fact that the dimensions for different specimens overlap is best shown in Figure 2. The differences between the aeciospore species means are relatively much smaller than the differences which were found in the case of the tubercles and peridial cells. These points are evident after an examination of the probability constants shown in Table 5. The difference in

spore length between the two species means, though only 10 per cent, is more than 11 times its probable error, and on the face of things is undoubtedly significant. In spore width, wall thickness, and ratio $\frac{\text{mean length}}{\text{mean width}}$ the two species show less decisive differences with respect to their probable errors. In any case differences in these other characters do not furnish entirely independent support of the species difference, because all three factors are correlated with length. For *Cronartium ribicola* aeciospore lengths the correlation coefficient with width is 0.59 ± 0.09, and with wall thickness 0.61 ± 0.10. For *C. occidentale* lengths the correlation with width is 0.54 ± 0.11, with wall thickness 0.53 ± 0.13, and with the ratio of length to width 0.43 ± 0.12.

There remains the question as to whether the significant difference between the two populations sampled as to aeciospore lengths is really genetic, or simply due to differences in climate or substratum. These are questions on which the above probability figures give no information. The possibility that the larger spores of *Cronartium occidentale* are due to climatic influence can be practically ignored for the reason that it grows in a much drier climate than that in which the *C. ribicola* collections were made; and it is the general observation that the effect of drought, if any, is to decrease spore size. It is less easy to dispose of the possibility that the difference is due to substratum. So far as one can judge, if there had been more *C. ribicola* measurements from *Pinus monticola* the difference in average spore length between the two rust species would have been less. In the same way *C. occidentale* produced spores on *P. edulis* which differed less from *C. ribicola* than did those on *P. monophylla*. The aeciospore measurements are summarized separately by hosts in Table 6.

In the case of *Cronartium ribicola* it is impossible to reach definite conclusions as to the meaning of the difference between the spores from the two hosts, though all three of the specimens from *Pinus monticola* have larger spores than the mean of the spores from *P. strobus*, and the best probability computations possible under the circumstances indicate the difference to be significant. The specimens of *C. occidentale* were more evenly divided between its two hosts. The difference between the mean length of the aeciospores from *P. monophylla* and from *P. edulis* is scarcely more than twice its probable error. If the spores produced on *P. monophylla* are regularly larger, it is evident that measurements must be made from a larger number of specimens to establish the fact. Within each fungus species the difference between spore lengths from different hosts is small as compared with the difference in spore length between the species. The evidence is strong, though not absolutely conclusive, that irrespective of hosts, the spores of *C. occidentale* are longer than those of *C. ribicola*. To make it conclusive, it would be necessary to have measurements of each fungus from several congenial hosts. The ideal would be to have for comparison measurements of both fungi on a common congenial host, but it is very improbable that such a host exists. The wide spores and thick walls produced on *P. monticola* may indicate substratum effect, but perhaps they are the result of variation in sampling, of the moist atmosphere of Vancouver, or of an especially large-spored tendency in the strain of *C. ribicola* in

the single nursery-stock shipment which was the source of the Vancouver rust epidemic. Substratum effect is the most likely explanation, as the single specimen on *P. strobus* from Vancouver was decidedly below average in all the qualities in which the specimens from *P. monticola* were so high. There was striking agreement between the three *P. monticola* specimens in wall thickness; the possibility of poor sampling of the spores from the specimens measured was decreased by measuring 200 each from two of the specimens instead of the usual 100.

It will be noted that the probability constants in Tables 5 and 6 are computed from the population of specimen means, and not from the measurements of the individual spores. The latter procedure has been the one usually followed in the application of probability computations to spore measurements. It is theoretically at once evident that such a practice is unsound, for the reason that a sample composed of numerous spores from each of several specimens is not a simple sample such as one must choose for ideal probability computations. It is further evident that the number of individuals included in the sample is indicated not by the number of spores, but by the number of specimens. To substitute the number of spores for N in the denominator of the probable error formula will therefore give too low a value for the error. Empirical evidence of the lack of meaning of the probable error computed in the usual way from the individual spore measurements can be readily obtained from the data in the present paper. The error of the mean of the first 2,000 measurements of aeciospore lengths which were made for *C. ribicola* is 0.038μ. If this were valid for the species, the probable deviation of a mean of 100 measurements from the species mean should be $(2{,}000/100)^{\frac{1}{2}} \times 0.038\mu$ or 0.17μ. As a matter of fact, of the 20 specimen means, 17 show a larger deviation. Proceeding in the same way, it is found that 18 of the first 20 specimen means of *C. occidentale* differ from the species mean by more than the probable deviation (for this species 0.20μ). In fact, 11 of the 20 specimen means of the first fungus and 11 of the 20 means of the second actually differ from the species mean by more than three times the probable deviation figured from the 2,000-spore basis. In normal, simple populations only two such deviations would be expected in 47 submeans. It is undoubtedly true that means of 100 measurements taken at random from 20 or 25 different specimens would not so radically exceed the probable deviation; but it nevertheless appears that the only conservative procedure in calculating probability constants applicable to such a group as a species is to compute probable deviations or errors from a population of specimen means rather than from a population of individual measurements. In the present case the probable errors so computed are nearly four times as large as those obtained from the individual measurements, and the deviations of the specimen means quite closely follow the expectations based on these larger errors.

THE USE OF THE BIOMETRIC DATA IN THE IDENTIFICATION OF UNKNOWN SPECIMENS

Because the aecial stages of the two rusts have in the past inhabited different geographic regions and different hosts, there has been so far no need for microscopic identification of specimens. With the spread of *Cronartium ribicola* in the western part of the United States

the geographic criterion will no longer be valid, and it is entirely possible that either rust may be found capable of infecting one of the aecial hosts on which the other occurs. To avoid possible future confusion in the campaign which is being made for the control of *C. ribicola* in the West, it is desirable that there be available as many diagnostic criteria as possible. This is particularly true since some of the criteria may be changed as a result of change of host, and others, such as those dependent on the peridia, may be unavailable in weathered specimens. The size of the tubercles on the aeciospores is probably the character which may be depended on as most reliable and always available for examination. However, its determination requires very high magnification, and the aeciospores themselves will ordinarily be the character first measured. Because the differences between the two species in the dimensions of the aeciospores are small, the most probable diagnostic division point between them has been determined. Variability and probability constants based on the populations of specimen means—not of individual measurements—were employed in the determination. Obviously, if two species are equally variable the division point will be halfway between them; but if one species is more variable than the other, the division point should be farther from it and nearer the less variable species. The distance of the division point from each species mean should be proportional to the variability of the species. The division point located by the method described in the following paragraph is believed to have a higher probability of correctness than that determined by the inspection method used in earlier work with the uredinial stages of the two fungi (*3*).

The point is to be so located that the probability of a mean of measurements from a specimen of the smaller spored species being *above* the point would be equal to the probability of a specimen mean from the larger spored species being *below* the point. If A is the mean of the population of means for the larger spored species, B the mean for the smaller spored, σ_a the standard deviation of the A population, σ_b the standard deviation of the B population, and X the diagnostic division point, the conditions of probability referred to may be expressed by the formula

$$\frac{A-X}{\sigma_a}=\frac{X-B}{\sigma_b}$$

Solving for X[4]:

$$\sigma_b A-\sigma_b X=\sigma_a X-\sigma_a B$$

$$X(\sigma_a+\sigma_b)=\sigma_b A+\sigma_a B$$

$$X=\frac{\sigma_b A+\sigma_a B}{\sigma_a+\sigma_b}$$

Substituting the values for aeciospore length recorded in Table 1

$$X=\frac{(1.11\times 26.8)+(1.18\times 24.2)}{1.18+1.11}$$

$$=25.46$$

[4] The writers are indebted to T. R. C. Wilson for an improvement in the formula which they originally used for this purpose.

The probable deviation or error of a single specimen can be used in the formula in place of the standard deviation without affecting the result. The average deviation may also be used without serious loss of accuracy.

The diagnostic division point for aeciospore length, 25.46, is distant from the means 26.8 and 24.2 by approximately 1.66 times the probable deviations of single specimen 100-spore means, 0.81 and 0.76, respectively, for the two species. A deviation 1.66 times the probable deviation would be expected approximately 26 times in 100 trials, and only 13 times in the direction of the diagnostic division point. Assuming that the distribution approaches normal and that the specimens are in each case a good sample of their species, the chances are that about 13 per cent of all specimens diagnosed on the basis of the length mean would be diagnosed incorrectly.

The diagnostic division points obtained in this way for the other characters measured are shown in Table 5. For the ratios of length to width, variability and probability computations based on the logs of the specimen ratios would be somewhat preferable; but the variability in the ratios is small enough so that the differences in the results would be negligible. From the probability data, it appears that the chances of wrong diagnosis are approximately 36 per cent on the basis of width, 32 per cent on the basis of wall thickness, and 30 per cent on the basis of the $\frac{\text{mean length}}{\text{mean width}}$ ratio. The possibility of wrong diagnosis from the dimensions of aeciospore tubercles and of the peridial cells would be negligible.

Of course it must be understood that the bases for all these probability computations are inadequate in the number of specimens represented to justify entire confidence in them. The reliability of the figures given is also somewhat lessened by the fact that the specimens of each species have been treated as simple samples of a homogeneous population, when it is entirely possible that additional data would have shown that the measurements of each fungus are significantly affected by differences in host species. The diagnostic division points and the probability figures simply are the best results that can be condensed out of the available data. The actual number of specimens of the material investigated that would have been wrongly determined by application of the diagnostic division points is 6 out of 46 for aeciospore length, 16 out of 45 for width, 12 out of 33 for wall thickness, and 9 out of 45 for ratio $\frac{\text{mean length}}{\text{mean width}}$. None of the specimens whose aeciospore markings and peridial cells were measured would have been diagnosed wrongly on the basis of the dimensions of these structures.

The length, width, and $\frac{\text{mean length}}{\text{mean width}}$ data from Table 1 are shown graphically in Figure 2. Each plotted point represents both the mean length and the mean width of 100 measurements; in other words, the mean size of 100 spores. For example, the solid dot at the intersection of loci 24.4 and 17.9 represents the length and width means of *Cronartium ribicola* from Dunraven, N. Y. (See Table 1.) The stars represent the species means. The vertical line at 25.46 represents the diagnostic division for length, the horizontal line at 18.68 represents the point for width, and the solid diagonal line

drawn to satisfy the equation, length = 1.365 width represents the division for $\frac{\text{mean length}}{\text{mean width}}$. The figure serves much better than a table to illustrate the way the mean sizes of the spores from different specimens vary from the species mean and with respect to the diagnostic division lines, and the extent to which the ranges of the two species overlap. For biometric diagnosis, length appears from every viewpoint to be the most important of the aeciospore dimension criteria so far discussed, and if one were called upon to make a diagnosis of a white pine or nut pine Peridermium after an examination of the spore dimensions alone the length criterion would naturally be applied first.

A SINGLE DIAGNOSTIC INDEX WHICH USES BOTH LENGTH AND WIDTH

It will be noted that the line on Figure 2 which represents the most probable separation of the two species on the basis of spore length is vertical, that for width is horizontal, and that for the ratio of length to width has its origin at 0 for both length and width. It is at once evident that the line which will best separate the two "swarms" of specimen means shown in the graph will rarely happen to be an exactly horizontal or vertical line, or one which starts at zero for both length and width. It is evident from the graph, and has been confirmed by the coefficients given on page 524, that length, width, and their ratio are so correlated within each swarm that the criteria are not independent, and there is little advantage in trying to employ them separately for diagnostic purposes. In such cases the writers recommend that the line which seems best to separate the two swarms be located by inspection. The broken diagonal line in Figure 2 was so located. For all points on the line, length is $15.5\mu + 0.553$ width. This value was found after the line had been located, by noting that it cut the zero width line at 15.5 on the length scale, and increased 0.553μ on the length scale for each 1μ increase on the width scale. Its significance is that if a specimen has spores whose average length is more than $15.5\mu + 0.553$ of their average width, it is considered as probably *Cronartium occidentale;* if the average length is less than this value, the specimen is probably *C. ribicola.* Of the 45 specimens for which both lengths and widths are available, it will be seen on the graph that 4 would be wrongly identified by this criterion. For this particular lot of data, the vertical diagnostic length line happens to separate the swarms nearly as well as any other line which can be drawn.

While the slope of this line has been decided by inspection, it has been pivoted on the intersection of the most probable division values for length and width, and is probably more accurate than if located entirely by inspection. Its slope could be determined mathematically by describing for each swarm a contour of the best fitting frequency surface for that swarm. The points at which the contours for the two swarms intersect would be loci of the most probable, or at least of a very probable, straight line of separation. It is difficult to imagine any situation in mycological work which would justify the amount of computation required by such a process.

Where the correlation between length and width is not rectilinear, or where the two swarms differ materially in shape or degree of spread

the best line of separation of two swarms will be a curve. The determination of the best curved line would be a still more difficult matter, and the advantage over a straight line, if any, would probably be slight.

GENERAL DISCUSSION

One of the populations which have been compared in the present paper has included Cronartium individuals occurring on a 5-needled pine in the northeastern part of the United States, together with a smaller population on this and another 5-needled pine in British Columbia. The other population has included Cronartium individuals which grow on two nut pines in the southwestern part of the United States. The two populations were at one time confused; they were classed as separate species, chiefly on the ground of differences in host preference. In an earlier paper one of the present writers has shown that there is a small quantitative morphologic difference between the two fungi in the urediniospores when grown under outdoor conditions, whether in their respective natural habitats, or as a result of inoculation on the same hosts and under the same conditions. The data in the present paper show that the aecial stages differ very strikingly in some morphologic characters, and in others display smaller differences which by biometric methods can be shown to be significant. The differences which are so large that biometric demonstration is not required are of course the most important ones from every standpoint. It has not been possible in the aecial-stage comparisons to eliminate the possible influence of different climate or host, but the evidence indicates that the major portion of the differences observed are genetic, rather than the effect of environment or substratum. Added to the differences which had previously been demonstrated (*5*), these aecial differences seem sufficient to end any question as to the independent specific rank of *C. occidentale*.

These morphologic differences in the aecial stage should also be helpful in situations which may require the determination of specimens from unidentified host bark, or where there is suspicion that one of the species has jumped to a host outside of its usual host range. It is well to point out, however, that unless methods strictly comparable to those used in this paper are employed, other investigators can not expect the means and diagnostic division points to hold good, and they will have to rely on the qualitative morphologic differences for diagnosis.

The following descriptions of the aeciospores and peridia of the two forms combine the morphologic and biometric data. The figures are the same as, or are based on, the averages of the populations of means shown in Table 1:

Cronartium ribicola Fischer—

Peridia thick, persistent; 3 to 5 cells thick; outer layer of cells in region near dome, sectional view, long and short dimensions (basis 100 measurements from each of 8 specimens) 41.4 by 28.5μ, standard range [5] of the 8 specimen means, 39–43.8 by 26.3–30.7μ; outer wall of cells in outer layer smooth 7.16μ thick, generally thicker than inner wall; inner wall marked with short

[5] The lower and upper limits of the standard range differ from the mean by the amount of the standard deviation. Ordinarily about two-thirds of the specimens should have measurements within the standard range.

tubercles; outer walls of cells in second and third layers sometimes smooth, sometimes minutely warted, inner walls marked with tubercles; walls of cells in the inner layers generally uniformly marked with tubercles; walls progressively thinner from the outer layer to the inner layer of the peridium; outer walls of cells in first two or three layers usually thicker than the inner walls.

Aeciospores obovoid to ellipsoid, generally smoothly curved in outline, (basis 100 spores from each of 25 specimens) 24.2 by 18.3μ, standard range of the means 23.1–25.3 by 17.2–19.4μ; ratio mean length divided by mean width, geometric mean of the values for the 25 specimens 1.32; wall (basis 100 spores from each of 19 specimens) 3.41μ; wall partly smooth and partly marked with tubercles, the smooth area fissured near junction with tubercles; tubercles fairly regular in outline in end view (basis 100 measurements from each of 7 specimens), 1.52 by 1.10μ, standard range of the means 1.45–1.59 by 1.06–1.14μ.

Cronartium occidentale Hedg. Bethel, and Hunt—

Peridia thin, evanescent; one cell, rarely two cells thick; outer layer of cells in region near dome, sectional view, long and short dimensions (basis 100 measurements from each of 5 specimens) 27.4 by 19.1μ, standard range of the means 26.3–28.5 by 18.2–20.0μ; outer wall of outer layer of peridial cells 4.68μ; outer wall of cells in outer layer smooth, inner wall generally smooth, occasionally marked with minute tubercles; "concomitant" cells just below outer layer of cells of peridium (basis 100 measurements from each of 5 specimens) 21.9 by 17.9μ; standard range of the means 21.6–22.19 by 17.5–18.3μ; wall of concomitant cells 4.60μ; tubercles minute in end view, averaging somewhat less than 1 by 1μ, often compacted into irregular clumps.

Aeciospores obovoid to ellipsoid, often somewhat irregular in outline (basis 100 spores from each of 20 specimens) 26.8[6] by 19μ; standard range of the means 25.6–28 by 18–20μ; ratio mean length divided by mean width, geometric means of the values for the 20 specimens, 1.41; wall (basis 100 spores from each of 14 specimens) 3.85μ; wall partly smooth and partly marked with tubercles, the smooth area fissured near junction with the tubercles; tubercles irregular in outline in end view (100 measurements from each of 5 specimens) 2.29 by 1.33μ; standard range of the means 2.23–2.35 by 1.31–1.35μ.

A comparison between Figure 2 of the present paper and Figure 4 of the urediniospore paper (*3*) reveals the fact that the urediniospores and the aeciospores of *Cronartium occidentale*, respectively, differ in size and shape from the urediniospores and aeciospores of *C. ribicola* in the same general way. Reduced to percentages based on mean spore size, the urediniospores of *C. ribicola* may be described as 93 per cent as long as those of *C. occidentale*, and the aeciospores of *C. ribicola* as 90 per cent as long as those of *C. occidentale*. Whether this same general relation holds for the teliospores and sporidia remains to be seen.

None of the measurement distributions encountered gave indications of real bimodality. Skewness was more commonly positive; no extreme tendency to skewness was seen.

In the case of two forms which are as close together in their host relationships and morphology as *Cronartium ribicola* and *C. occidentale*, extreme spore-size ranges are utterly useless for diagnostic purposes. The statement in an earlier paper (*1*, *p. 632*) that the mature aeciospores of *C. ribicola* measure "18 to 21 by 20 to 26μ" tells only part of the story. In the present study, for instance, the extreme ranges for *C. ribicola* and *C. occidentale* are 16–43 by 11–25μ and 19–40 by 9–28μ, respectively. In which species would spores described by the first range cited be placed? The critical case presented by these two Cronartium species serves excellently to illustrate the fact that averages are more useful than ranges in certain types of taxonomic work.

[6] Length based on 21 specimen means.

SUMMARY

General observations have indicated marked differences in the habit of the aecia of *Cronartium ribicola* and *C. occidentale*. In the former the aecia are usually distinct sori with persistent peridia; but in the latter the aecia vary from distinct sori, e. g., on *Pinus monophylla*, to broad spore-bearing layers under the bark, e. g., as in infections on *Pinus edulis*, with thin inconspicuous peridia.

The aeciospores of *Cronartium occidentale* are slightly longer and wider than those of *C. ribicola;* they have a slightly thicker wall, a more irregular outline, and larger and more irregularly distributed tubercles.

The peridia of *Cronartium ribicola* are 3 to 5 cells thick, all the cells being marked with tubercles; the peridia of *C. occidentale*, on the other hand, are rarely more than 1 cell thick, and the cells in this one layer are rarely marked with tubercles. Certain cells, unlike the peridial cells or the aeciospores, are located just beneath the peridium of *C. occidentale*. These cells are given the name "concomitant cells."

Any unweathered specimen of *Cronartium occidentale* can be distinguished from any specimen of *C. ribicola* by any one of the following characters: Length, width, or shape of aeciospore tubercles; length or width of outer peridial cells; smoothness of outer peridial cells; and the contrast between concomitant cells and the cells above and below them. In aeciospore lengths, and in the gross characters of the sori, it is usually possible to distinguish between the two species, but in occasional specimens the two rusts overlap in these two characters.

The morphologic differences between *Cronartium ribicola* and *C. occidentale* seem quite sufficient to justify their standing as separate species.

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